

THE ELECTROCARDIOGRAM OF ARENICOLA

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There is evidence, on the basis of the accelerating action of acetylcholine, that the hearts of *Arenicola* and *Lumbricus* are neurogenic (Prosser and Zimmerman, 1943). Nerve cells, which may be pacemakers, are present in the hearts of *Arenicola* (Carlson, 1908). Another test of the nature of the pacemaker is the electrocardiogram (ECG) which in myogenic hearts (vertebrates and molluscs) consists of regular slow potentials and in neurogenic hearts (*Limulus*, decapod Crustacea, some insects) is oscillatory. The electrocardiogram of arthropods may, in addition, have slow components but the oscillations appear to correspond with the repetitive discharge of the pacemaker neurons (see Prosser *et al.*, 1950, for references). The electrocardiographic test of the pacemaker has not been applied to annelids and, in fact, no electrocardiograms of annelids have been published.

Electrocardiograms of *Arenicola* were recorded with an Offner amplifier and cryograph; the amplifier was capacity coupled and of variable time constants, the longest being 0.2 seconds. Electrodes were of silver-silver chloride either in direct contact with the tissue or connected by cotton wicks soaked in sea water. Efforts to record electrocardiograms from *Lumbricus* and *Neanthes* were unsuccessful but extensive records were obtained from the hearts of six large specimens of *Arenicola cristata*. The worms were anesthetized with chloretone, the two hearts were exposed and recovery from the anesthesia was permitted in running sea water as described by Prosser and Zimmerman (1943). One worm was pinned to a paraffin block and the hearts exposed without anesthesia, but excessive body movement resulted in an unsatisfactory preparation. Usually an indifferent electrode was placed on the liver or inner body wall and an active electrode was put on different parts of a heart, from the lateral gastric vessel down to the ventral end. There was much interference with electrocardiograms by slow potentials arising from movements of the intestine and muscles of the body wall, and it was necessary to make many records from each animal with varying electrode positions, several time constants and different states of recovery from anesthesia to obtain a consistent picture of the electrocardiogram.

Several typical records are shown in Figure 1. The electrocardiogram (ECG) of *Arenicola cristata* consists of an initial rapid negative wave followed by a positive deflection, often with several superimposed oscillations (1a, 1b, 1c, 1e, 1f). The number, duration and shape of the oscillations are variable and they usually terminate with a sharp negative spike (1c, 1e) which may be followed by a slow negative wave (1d, 1f). The precise form varies in the same locus from time to time and from one region to another; such variability is more characteristic of oscillatory than of slow-wave types of electrocardiogram. If slow potentials had been present, the amplifier would have detected them as shown by the slow potentials recorded

from hearts of squid and mussel (Fig. 2) and the many interfering slow potentials from body wall and intestinal muscle.

In *Arenicola* the beat normally starts in the lateral gastric vessel and spreads ventrally over the heart. Records taken from the dorsal portion (lateral gastric vessel) and from middle and ventral regions were qualitatively similar and showed no greater differences than did records from the same region at different times during a two-hour period of observation. Similar records were obtained whether wicks or wires made contact and electrode movement was so slight that it did not introduce an artifact. Regular electrocardiograms were occasionally observed when there was no visible contraction.

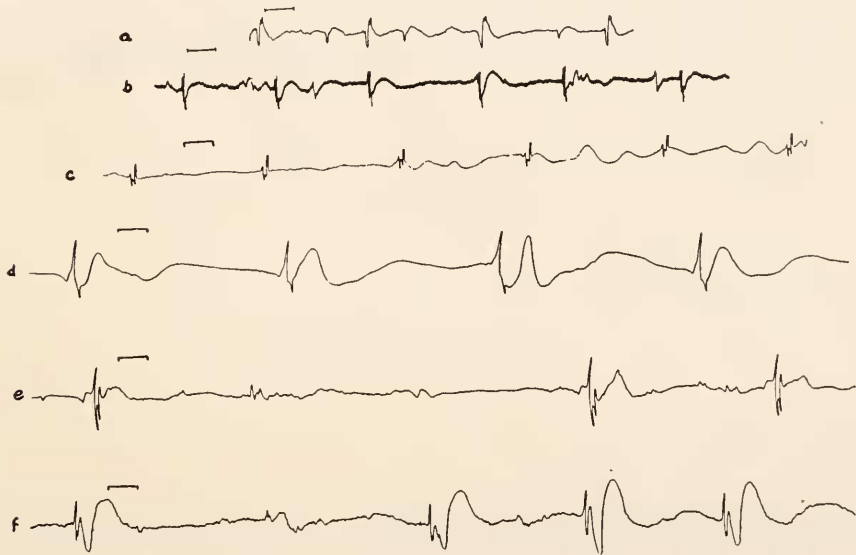


FIGURE 1. Electrocardiograms from *Arenicola*. Monopolar recording. In all records except 1a an upward deflection indicates negativity of the heart lead. 1a and 1b from same animal, all others different individuals. Time mark 1 second. In 1a three downward deflections between electrocardiograms were caused by activity of somatic musculature. Long time constant for records 1d and 1f, short time constants for other records. Note oscillatory spikes in 1a, 1b, 1c and 1f.

It was not possible to obtain a mechanical record of the contraction simultaneously with the electrical record. However, the heart was closely observed and the dilation and systole marked on the moving recording paper. The fast, initial component of the ECG consistently occurred before or simultaneously with dilation and the systole occurred later, often during the slow wave. Whether the fast potential is an action potential associated with active dilation, or whether there is a comparatively long delay between the action potential and systolic contraction is not certain, but the latter alternative seems more likely.

For comparison with *Arenicola* the electrocardiograms of known neurogenic hearts (*Limulus* and the spider crab *Libinia*) and known myogenic hearts (*Loligo*

and a fresh-water mussel *Amblema*) are given in Figure 2. The records from *Limulus* (Fig. 2a, b) resemble string galvanometer records (Garrey, 1932) and the one from *Libinia* (Fig. 2c) resembles records from *Astacus* (Hoffman, 1911), while the molluscan electrocardiograms (Figs. 2d, e, f) resemble records from *Octopus* (Luisada, 1932) and *Ostrea* (Taylor and Walzl, 1941). The electrocardiograms of *Arenicola* do not have the persistent oscillations of the arthropods but they do show several variable spikes and lack the large regular slow waves of molluscs and vertebrates. In one preparation a long series of spikes appeared without any visible beat: such irregular spikes are sometimes found in records from *Limulus* hearts.

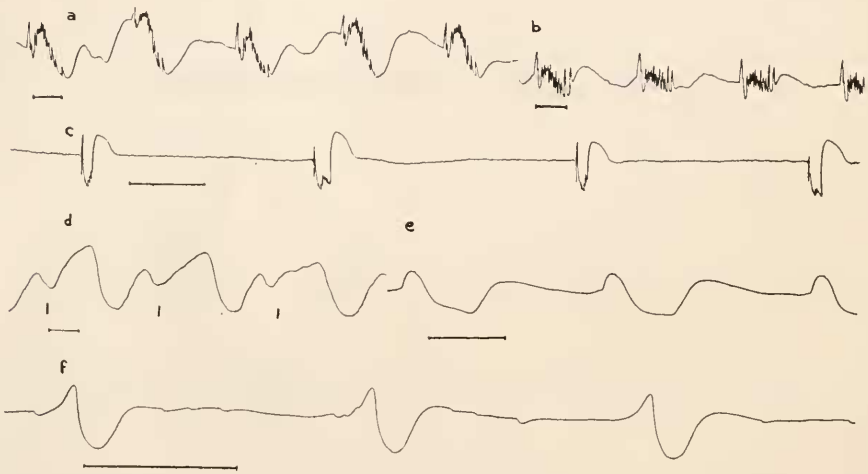


FIGURE 2. Electrocardiograms from neurogenic and myogenic hearts. Monopolar recording, upward deflection indicates negativity of active lead. 2a, c, d, e long time constant, 2b short time constant. Time records 1 second. a, b, *Limulus*. c, spider crab *Libinia*. d, e, fresh-water mussel *Amblema*. f, gill heart of squid *Loligo*. In 2d three vertical lines indicate point of systole. Note oscillatory spikes in 2a, 2b, 2c and presence of slow waves only in 2d, e and f.

It appears, therefore, that the electrocardiogram of *Arenicola* consists of summated spike potentials which may correspond to discharges from a ganglionic pacemaker. The fast components may be followed by a slow potential, the nature of which is as uncertain as it is in arthropod hearts. The electrocardiogram supports the hypothesis that the heart of *Arenicola* is neurogenic.

SUMMARY

The electrocardiogram of *Arenicola cristata* consists of a rapid negative deflection followed by a positive deflection, often with superimposed oscillations and often followed by a slow negative wave. There is much variability from animal to animal and from time to time at the same position.

The oscillatory nature of the electrocardiogram supports the hypothesis that the heart of *Arenicola* is neurogenic.

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